Tokushiro TAKASO*: **A developmental study of the integument in Gymnosperms (2)** *Pinus thunbergii* Parl., *Abies mariesii* Mast. and *A. veitchii* Lindl.**

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(Pl. III～IV)

Introduction This is the second part of a series of papers in which the histogenesis of integument of gymnosperms is described. In the first part (Takaso, 1980), I have reported on *Ginkgo biloba*. The present paper deals with three species of the Pinaceae, *Pinus thunbergii* Parl., *Abies mariesii* Mast. and *A. veitchii* Lindl. The morphological and histological features of the integument in *Pinus* and *Abies* were described by Doyle and O'leary (1935b), Doyle and Kane (1943), Doyle (1945), McWilliam (1958), etc. in their papers which dealt primarily with pollination mechanism. Some additional facts on the development of the integument have also been reported by Ferguson (1904), Quisumbing (1925), Konar and Ramchandani (1958), etc. However, our knowledge on the early ontogeny of the integument is not yet sufficient.

Materials and methods Table 1 gives data for plants from which specimens were collected for the present study: they are localities, numbers of trees used

Table 1. Data on materials

Taxon	Locality	Number of trees utilized	Season of collection
Pinus thunbergii	The Imperial Palace, Tokyo (cult.)	10	mid-April ～early May
Abies mariesii	Mt. Tengu and Mt. Yokote, Nagano Pref.	5	mid-May ～mid-June
A. veitchii	Mt. Tengu and Mt. Yokote, Nagano Pref.	5	mid-May ～mid-June

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and seasons of collection. Methods of making preparations for observations with light and scanning electron microscopes should be referred to my previous paper (Takaso, 1980).

Terminology Developmental features of the integument vary with positions on a developing ovule. The terms, i.e. the upper and lower, are used for describing the ontogeny of the integument (Fig. 1) : the "upper" refers to a position distant from the base of the ovuliferous scale, and the "lower" to a position close to that base. Thus, the ovular surface is divided into the upper side, lower side and lateral sides, the third of which refer to areas between the upper and lower sides. In the same way, each portion of the integument is expressed as the upper part (up), lower part (lw) and lateral parts (lt) (Fig. 1). Additionally, terms such as the apical part and basal part are also used in the description of a developing integument. They should be applied to parts of the integument relating to its apex and base, respectively.

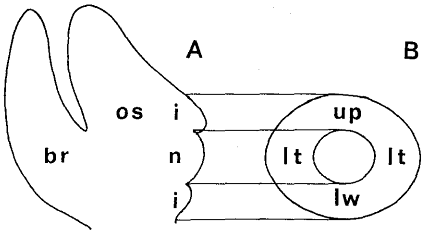

Fig. 1. Diagrammatic illustrations of the developing ovule in the Pinaceae. A. Longisection showing the relation of the ovuliferous scale and its associated bract. B. Adaxial view of the ovular apex, showing the upper (*up*), lower (*lw*) and lateral (*lt*) parts of the integument. See text for further explanation. (*br*: bract; *i*: integument; *os*: ovuliferous scale; *n*: nucellus; these abbreviations are common in the following figures.)

In the present paper, descriptions of the histological features of the integument are based largely on the median longisection of the ovule. The median longisection, which includes the apical part of the nucellus of an ovule, is obtained in one of serial radial longisections of a cone.

Observations The female cone of the Pinaceae has many spirally arranged bracts on the main axis, each bract subtending an ovuliferous scale which bears two ovules on its adaxial side.

Pinus thunbergii

Ovule primordium: Before the initiation of ovule primordia, an ovuliferous

scale is rounded triangular seeing from the adaxial side, and its tip is somewhat projecting upward (Pl. Ⅲ, A). Two ovule primordia are borne at the basal part of the ovuliferous scale with their apices pointing toward the main axis of the cone (Pl. Ⅲ, A). The first sign of the initiation of the ovule primordium is a swelling, and it differentiates later into the nucellus and integument.

Initiation of the integument: The initiation of the integument can also be recognized as the "swelling" which appears on the subapical part of the ovule primordium. As regards the position where the integument begins to swell, the following two cases are recognized. One is the case in which it begins to swell at two places, i. e. on either of the lateral side of the ovule primordium (Pl. Ⅲ, B) as described already by Baillon (1860) and Strasburger (1872, 1879). The other is the case in which it begins to swell simultaneously on all other sides except the lower, so that the swelling takes the form of a horseshoe in outline (Pl. Ⅲ, C). In any case, however, the swelling of the integument soon extends wholly around the nucellus except for the area of the nucellar apex, forming a ring in outline.

A median longisection of an ovule primordium (Fig. 3A) shows that cell divisions take place sporadically in the surface cell layer and inner region. In this stage the ovule primordium may be wholly meristematic in nature. At the stage when the integument and nucellus are being initiated, cells of the surface layer exclusively undergo periclinal divisions (see arrows in Figs. 2B and 3B; Table 2). Periclinal divisions may sometimes occur in cells of the inner region as well (Fig. 2B). Quisumbing (1925) stated that in *Pinus Banksiana* the integument was of "hypodermal" origin. According to the present observations, however, there is no doubt that the surface cell layer contributes to the swelling of the integument by periclinal divisions, at least so far as *Pinus thunbergii* is concerned.

Development of the integument: The young integument which has become ring form elongates rapidly. The pattern of development, however, varies with parts of the integument. The development of the lateral parts predominates over that of the upper and lower parts. As a result, either of the lateral part of the integument becomes longer than the upper and lower parts. So, the developing integument begins to have two projections (Fig. 2C and Pl. Ⅲ, D; see also Baillon, 1860; Strasburger, 1872, 1879; Haan, 1920; Quisumbing, 1925; etc.). In the lateral parts of the integument at the early stage of development,

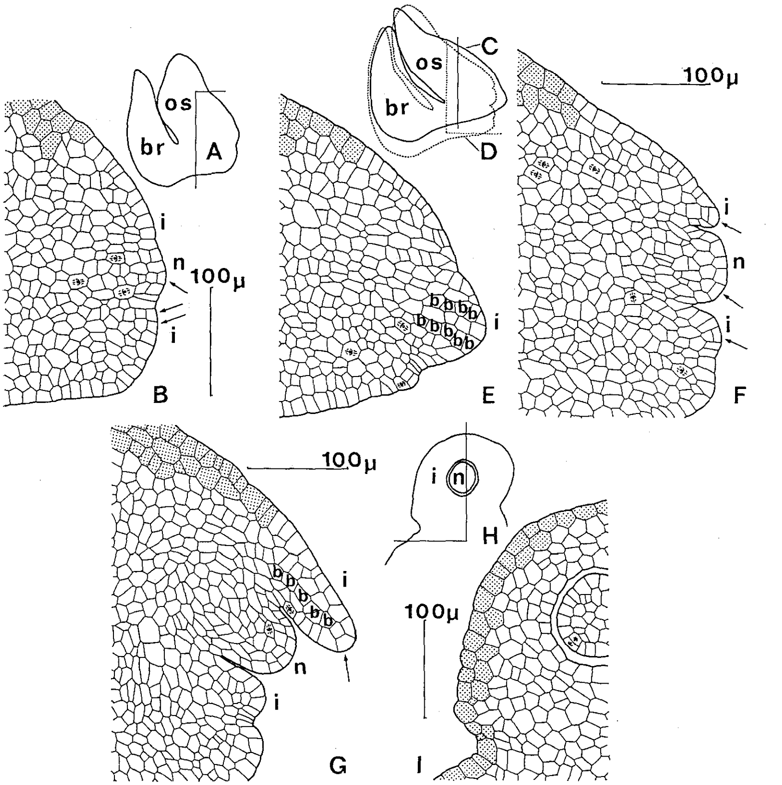

Fig. 2. *Pinus thunbergii.* Successive developmental stages of the integument. A and B. Median longisections of an ovule primordium, showing the initiation of the integument. A. Diagrammatic illustration. B. Details of area indicated in A. Arrows show periclinally divided cells in the surface cell layer. Cells of the surface layer are varied in size and shape. C–F. Longisections of a young ovule, showing the early development of the integument. C and E. Longisections through the lateral part of the integument. C. Diagrammatic illustration. E. Details of area indicated in C. Cell-rows marked *b* are those which have been resulted from successive periclinal cell divisions. D and F. Median longisections. D. Diagrammatic illustration. F. Details of area indicated in D. Arrows show periclinally divided cells in the surface cell layer of the integument and nucellus. G. Median longisection of a developing ovule. Cell-rows marked *b* have been resulted from successive cell divisions. An arrow indicates the periclinal cell division which has occurred in an apically situated cell of the surface layer of the integument. H and I. Cross sections of the basal part of a relatively developed integument. H. Diagrammatic illustration. I. Details of area indicated in H. Tannin becomes accumlated in cells of the outer surface layer of the integument. Dots indicate tanniferous cells being well stained with dyes (these dots mean the same as those in the following figures).

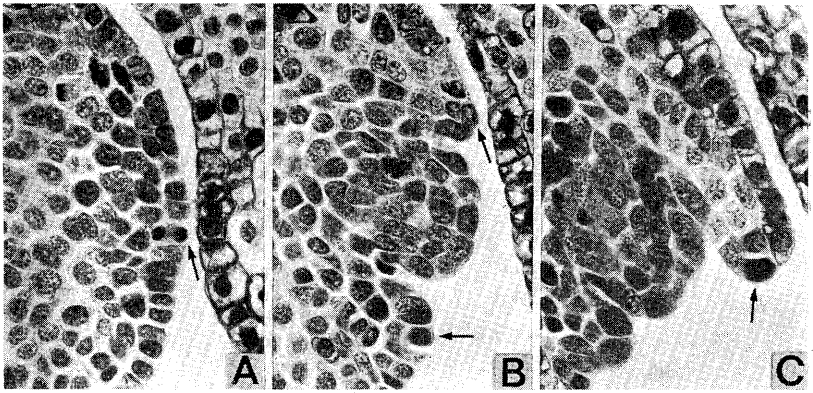

Fig. 3. *Pinus thunbergii*. Median longisections of an ovule primordium and young ovules, showing the development of the integument (A–C). Arrows show periclinal divisions in the surface cell layer. ×225.

cells of the surface layer as well as of the inner region frequently undergo periclinal divisions (Fig. 2E). Consequently, long cell-rows are formed (see cells marked *b* in Fig. 2E). In the upper and lower parts, however, periclinal divisions occur less frequently (see arrows in Figs. 2F and 3B; see also Table 2). In the surface cell layer of these parts, anticlinal cell divisions also sometimes take place.

As the development of the ovule proceeds, twin ovules begin to change their direction, the nucellar apices turning aside each other (Pl. III, D). During this period, the upper and lower parts of the integument exhibit fairly active development, though either of the lateral part is still longer than the upper and lower parts. The upper part of the integument is composed of long cell-rows. These long cell-rows are formed in the following manner: successive periclinal divisions take place in apically situated cells of the surface cell layer of the integument, and cells forming inner cell-rows of the integument show successive divisions, which are anticlinal to the surface of the integument, being accompanied with successive anticlinal divisions in the surface cell layer (see Fig. 3C; see also cells marked *b* in Fig. 2G).

In the relatively developed ovule, the lateral parts of the integument have thicker bases than the upper part (Figs. 2H and 5). This may be a result from the fact that the lateral parts have originally been initiated by more numerous cells than the upper and lower parts. Tannin becomes accumulated in cells of

the outer surface layer as well as in some outermost cells of the inner region of the integument (see dotted cells in Fig. 2I).

Mature ovule: An ovule is curved downward, though somewhat obliquely, and the upper half of itself is projecting from either side of the ovuliferous scale (Pl. III, E). The integument wholly envelops the nucellus and forms a micropyle with a large diameter. The apical part of the integument exhibits a unique morphology, i.e. a two-horned structure which has been resulted from the predominant development of the lateral parts (Pl. III, E, F; see also Ferguson, 1904; Doyle and O'leary, 1935b; Konar and Ramchandani, 1958; McWilliam, 1958; etc.). Additionally, the lower portion of each horn may usually be lobed coarsely (Pl. III, E, F).

The apical part of the integument is in most cases three cell-layered in thickness, and that of the basal part five to seven cell-layered (Ferguson, 1904; Quisumbing, 1925; McWilliam, 1958).

A longisection of the lateral part forming a horn (Fig. 4A) shows that the inner region is composed of very long cell-rows which have been resulted from the repetition of cell divisions which are anticlinal to the surface of the

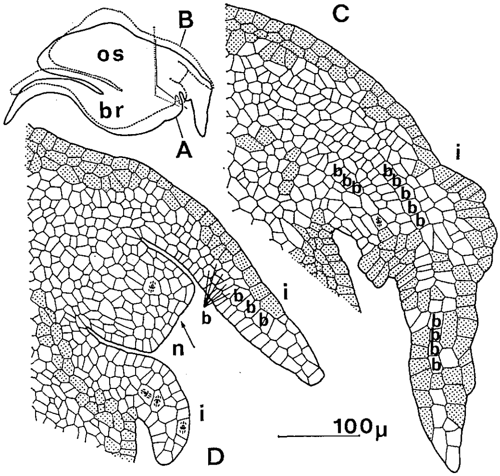

Fig. 4. *Pinus thunbergii*. Longisections of a mature ovule. A and C. Longisections through the lateral part of the integument. A. Diagrammatic illustration. C. Details of area indicated in A. B and D. Median longisections. B. Diagrammatic illustration. D. Details of area indicated in B. Long cell-rows marked *b* have been resulted from successive cell divisions. An arrow indicates a slight depression at the nucellar apex.

integument (see cells marked *b* in Fig. 4C). The similar feature is also observed in the upper part of the integument (Fig. 4D). In these cell-rows, particularly in those at the basal part, periclinal cell divisions may take place, increasing the thickness of the integument (Fig. 4D; see also Quisumbing, 1925). A slight depression is generally formed at the apex of the nucellus (see an arrow in Fig. 4D; see also Ferguson, 1904; Konar and Ramchandani, 1958).

After pollination, cells of the integument which are forming the micropyle rapidly elongate and enlarge, and close the micropyle (Fig. 6; see also Ferguson, 1904; Quisumbing, 1925; McWilliam, 1958; etc.).

Abies mariesii and A. veitchii

There is little difference in histological features of the integument between *Abies mariesii* and *A. veitchii*. They share many characteristics in common.

Ovule primordium: Viewed from the adaxial side, an ovuliferous scale looks fan-shaped in outline, and two ovule primordia are borne at its basal part. The initiation of each ovule primordium is recognized by a swelling as in *Pinus thunbergii* (Pl. IV, A).

Initiation of the integument: In *Abies veitchii* as well as in some specimens of *A. mariesii*, the integument is initiated as two distinct swellings from the subapical part of the ovule primordium (see arrows in Pl. IV, E). In *Abies mariesii*, however, swellings often arise simultaneously from various places (Pl. IV, B). As compared with *Pinus thunbergii*, two species of *Abies* have the swellings arising from broader areas on the ovule primordium (Fig. 7A and Pl. IV, E). In other words, the integument in *Abies mariesii* and *A. veitchii* is thicker than in *Pinus thunbergii* at the initial stage (Fig. 7B). The two or more swellings, which have been initiated separately, soon extend wholly around the nucellus except for the apex. During the subsequent stages of development, however, either of the laterál part of the integument predominates in development over the upper and lower parts, thus forming two remarkable projections as in *Pinus thunbergii*. Of the two projections one nearer to the supposed midrib of the ovuliferous scale is larger than the other (Pl. IV, C, F).

A cross section of an ovule primordium (Fig. 7A) in which the integument is being initiated shows that a lot of cells of the inner region take part in swellings of the integument; moreover, it shows that some apically situated cells of the surface cell layer contribute also to the swellings by their respective

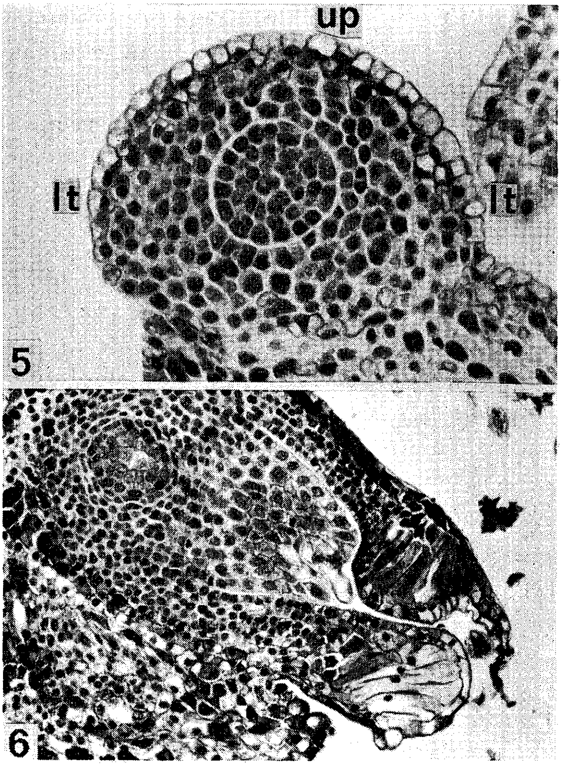

Fig. 5. *Pinus thunbergii*. Cross section of the basal part of a relatively developed ovule. The lateral parts (*lt*) are thicker than the upper part (*up*). ×170.
Fig. 6. *Pinus thunbergii*. Median longisection of an ovule after pollination. The micropyle is closed by elongation of cells constituting the integument. ×100.

periclinal divisions (see an arrow in Fig. 7B). Thus, cells of the surface layer of the integument frequently undergo periclinal divisions during the early ontogeny (Table 2). Similarly, cells of the surface layer of the young nucellus are also frequently divided periclinally (Fig. 7D; Table 2). The surface cell layer of the integument and nucellus is composed of various cells in shape and size (see cells marked *a* in Fig. 7B). In the inner region of the young nucellus lie many cell-rows which have been resulted from the repetition of cell divisions. Cell-rows are sporadically observed in the inner region of the young integument as well (see cells marked *b* in Fig. 7D, for example).

Development of the integument: For a considerably long time, two projec-

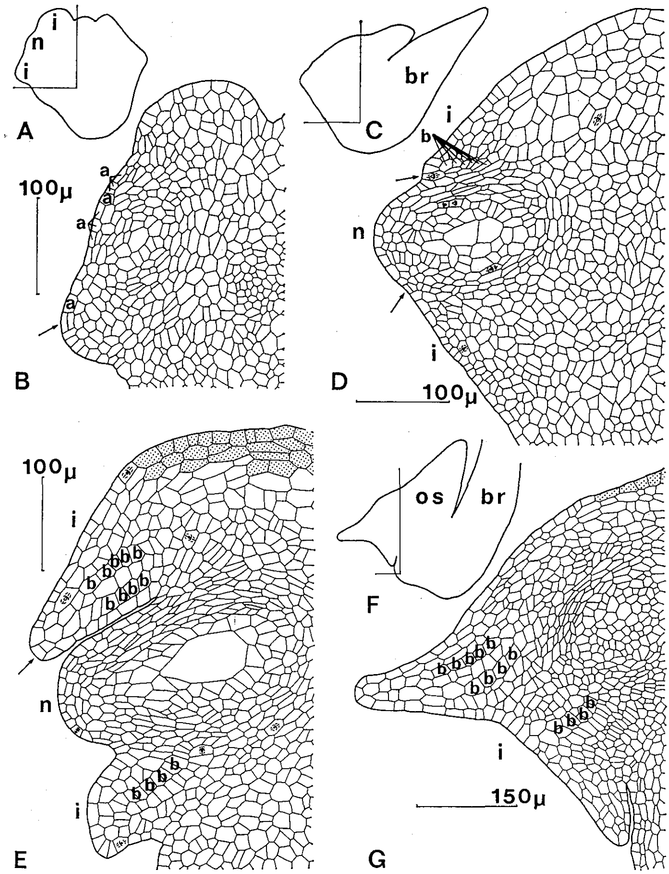

Fig. 7. *Abies veitchii* (A, B, F and G) and *A. mariesii* (C–E). Successive developmental stages of the integument. A and B. Cross sections of an ovule primordium, showing the initiation of the integument. A. Diagrammatic illustration. B. Details of area indicated in A. An arrow shows periclinally divided cells in the surface cell layer. Cells of the surface layer as marked *a* are varied in size and shape. C and D. Median longisections of an ovule primordium, showing the early development of the integument. C. Diagrammatic illustration. D. Details of area indicated in C. Arrows show periclinal divisions in the surface cell layer. Short cell-rows (as marked *b*, for example) are formed by successive cell divisions. E. Median longisection of a developing ovule. Cell-rows marked *b* are those which have been resulted from successive cell divisions. An arrow indicates the periclinal cell division which has occurred in an apically situated cell of the surface cell layer of the integument. F and G. Longisections through the lateral part of a developing integument. F. Diagrammatic illustration. G. Details of area indicated in F. Cell-rows are marked *b*.

tions formed by either of the lateral part are prominent (Pl. IV, G). In the later stages of development, however, the upper and lower parts show also highly active development. In the stage when the integument overgrows the nucellar apex, every part of the integument develops to the same degree. So, a state having the two projections is lost. During these later stages of development, twin ovules on the ovuliferous scale begin to change their direction, nucellar apices turning aside from each other (Pl. IV, G).

As the development of the ovule proceeds, periclinal cell divisions in the surface cell layer of the integument become restricted to its apical part (see an arrow in Fig. 7E). Cells of the inner region of the integument are somewhat larger than those of the nucellus, and are arranged in rows because they ha--

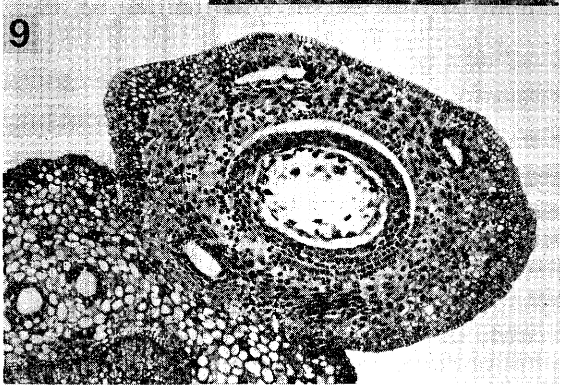

Fig. 8. *Abies mariesii*. Longisection of the upper part of a developing integument. Cells of the inner region are arranged in long rows. ×230.

Fig. 9. *Abies veitchii*. Cross section of the basal part of a mature ovule. The integument is thick, and resin canals are formed through the inner region. ×60.

mostly been formed by successive cell divisions (Fig. 8; see also cells marked *b* in Fig. 7E, G, for example). During the development of the nucellus, periclinal cell divisions sometimes take place in the surface cell layer (Fig. 7E). Short cell-rows exist sporadically in the inner region of the nucellus, however, they become gradually obscure.

Mature ovule: A mature ovule is curved with the upper-half emerging out of either side of the ovuliferous scale. This emerged or exposed upper-half is directed outward, i.e. in the opposite direction to the main axis of the cone (Pl. IV, D, H). A developed integument forms a micropyle with a relatively large diameter just above the nucellar apex. Every apical part of the integument is, however, curved backward, thus taking the form of a bugle (Doyle and Kane, 1943; Doyle, 1945). The tip of the integument may be coarsely lobed.

The apical part of the integument is three or four cell-layered in thickness, and the thickness increases gradually toward the basal part. The basal part of the integument consists of about 20 or more cell-layers. The basal part of the integument of *Abies mariesii* and *A. veitchii* is much thicker than that of *Pinus thunbergii*.

As an ovule matures, several histological changes occur in the integument and nucellus, as follows: (1) In the integument, cells of the outer epidermis, which is derived from the surface cell layer, as well as those of the subdermal two or three cell-layers become elongated and are stuffed with tannin (see dotted cells in Fig. 10B). (2) At the basal part of the integument, most cells of the inner region become enlarged and are tanniferous. Some cells at the base of each lateral part, however, keep their small size, and are not containing tannin (Fig. 10D). (3) Resin canals may differentiate in the inner region of the integument (marked *r* in Fig. 10D; see also Fig. 9). They are characteristically surrounded by small cells. (4) The apex of the nucellus frequently has a slight depression as in *Pinus thunbergii*.

After pollination, the apical part of the integument is folded and closes the micropyle as stated by Doyle and Kane (1943) and Doyle (1945).

Frequency of periclinally divided cells in the surface layer of the integument and nucellus: In the previous paper (Takaso, 1980), I have recorded the frequency of periclinally divided cells seen in the surface layer of the nucellus, integument and collar during the ontogeny of *Ginkgo biloba*. In the present study, a tentative examination was made on *Pinus thunbergii* and *Abies mariesii*

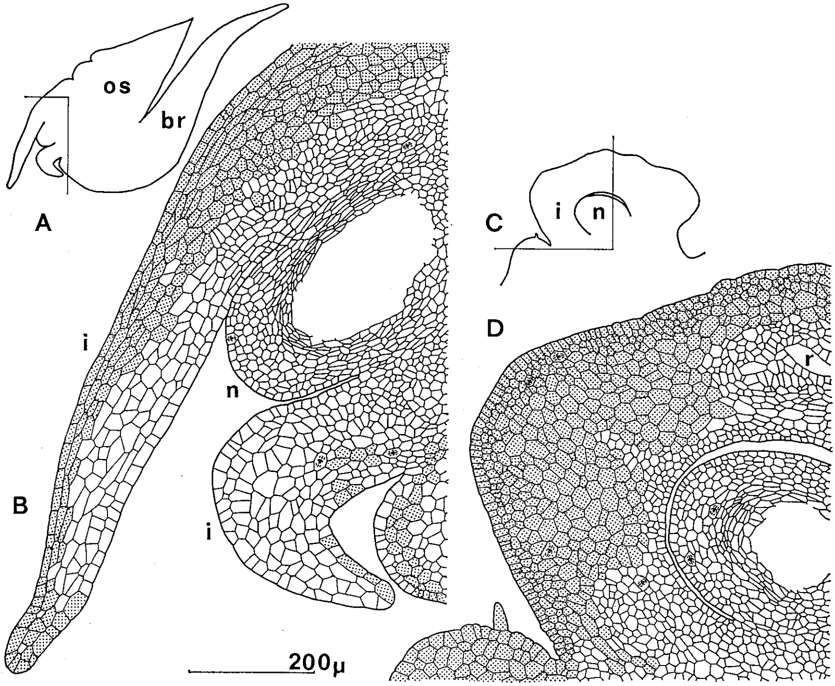

Fig. 10. *Abies mariesii*. Longi- and cross-sections of mature ovules. A and B. Median longisections. A. Diagrammatic illustration. B. Details of area indicated in A. C and D. Cross sections of the basal part. C. Diagrammatic illustration. D. Details of area indicated in C. Most cells of the integument are stuffed with tannin. A resin canal (marked *r*) is surrounded by a group of small cells in a cross section.

similarly.

The frequency was calculated in the ovules at the early stages of development, that is, from the stage in which the integument is initiated (as shown in Figs. 2A and 7C) to the later stage in which the swelling of the integument forms a continuous ring (as shown in Fig. 2C, D). Counting was made for the apical surface areas of the lateral, upper and lower parts of the integument as well as for the apical surface area of the nucellus respectively. Every other was taken out of serial longisections which were obtained through the lateral part, the upper-lower parts and the other lateral one (Fig. 12). Thus, six longisections per ovule were selected for the examination, each was cut about 10 μm in thickness. In the integument, five cells per section through the lateral

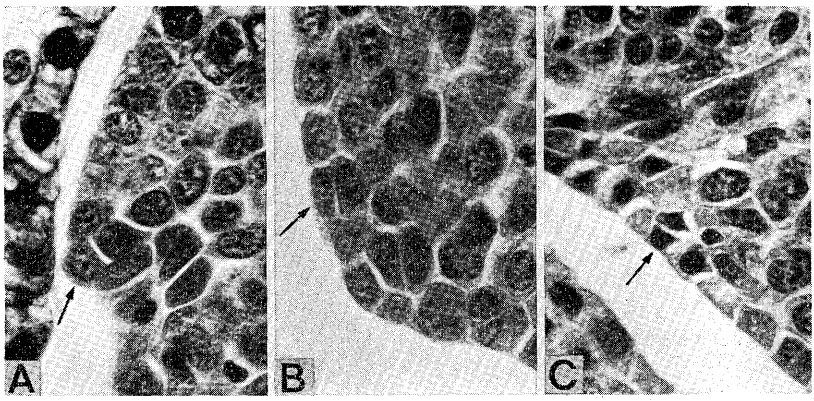

Fig. 11. Longisections of the integument, showing periclinally divided cells (arrows). A. Upper part of the integument in *Pinus thunbergii*. B. and C. Lateral and lower parts of the integument in *Abies mariesii* respectively. ×420.

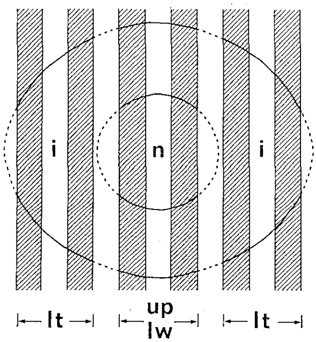

Fig. 12. Diagram of the adaxial view of a young ovule. Shaded six longisections per ovule were used for the calculation of the frequency of periclinally divided cells. See text for further explanation.

part, and 10 cells per section through the upper-lower parts (i. e. five cells at the upper and lower parts respectively) were examined, and in the nucellus, five cells per section through the nucellus. Examples of recently periclinally divided cells counted are shown in Fig. 11 A-C (see arrows).

The result is summarized in Table 2. In the both species the frequency is highest at the lateral parts of the integument, i. e. 34.6% in *Pinus thunbergii* and 17.8% in *Abies mariesii*, and lowest at the upper-lower parts of the integument, i. e. 9.6% in *Pinus thunbergii* and 3.5% in *Abies mariesii*. The frequency at the apex of the nucellus is intermediate between those at the lateral parts

Table 2. The frequency of periclinally divided cells in the surface layer of the integument and nucellus in the early stages of development. The frequency is given in the following formula.

Frequency

$$= \frac{\text{Number of mother cells which have divided periclinally}}{\text{Number of cells observed}} \times 100$$

The number of cells observed for each calculation is put in a bracket.

	Pinus thunbergii	*Abies mariesii*
Nucellus	19.2% (360)	13.9% (230)
Integument (lt*)	34.6% (635)	17.8% (325)
Integument (up-lw**)	9.6% (710)	3.5% (405)

*: Lateral parts of the integument.
**: Upper and lower parts of the integument.

and upper-lower parts of the integument. These values well represent the pattern of the early ontogeny of the ovule, particularly as to that of the integument.

If, in *Pinus thunbergii*, the origin of cells of the nucellus and integument is traced back to the primordial stage, a considerable amount of cells of them seems to have been derived from the surface cell layer of the ovule primordium. In *Abies mariesii*, however, a lot of cells of the inner region also contribute to the initiation of the integument and then to the subsequent development. The amount of cells of the integument and nucellus which have been derived from the surface cell layer may be less in *Abies mariesii* than in *Pinus thunbergii*.

Discussion Baillon (1860, 1864) and Strasburger (1872, 1879) reported on the place, where the swelling of the integument appears on the ovule primordium, in *Pinus resinosa*, *Larix europaea* and *Pinus Pumilio*. They stated that the integument arises as two swellings on either of the lateral side of the ovule primordium. In addition, the present observations have confirmed that the integument is initiated as two swellings also in *Pinus thunbergii*, *Abies mariesii* and *A. veitchii*. It is frequent, however, that the integument arises from all other sides except the lower (*Pinus thunbergii*) or from various places (*Abies mariesii*). In the former case the swelling appears in the shape of a horseshoe. In *Abies mariesii* ovuliferous scales and bracts are tightly piled on the main

axis. In this species physical pressure between an ovuliferous scale and a barct above the ovuliferous scale may cause the inconsistency of the place where the swelling appears on the ovule primordium.

Even though the integument in some specimens of *Abies mariesii* and *Pinus thunbergii* has not been initiated from two distinct places, the ovule always becomes to have two distinct projections due to the prominent elongation of either of the lateral part during the subsequent stages of development. This phenomenon is entirely the same as in the case where the integument is initiated originally at two distinct places. In *Pinus thunbergii* the two projections are kept on to the mature stage of development as reported by Strasburger (1872, 1879), Ferguson (1904), Quisumbing (1925), etc. In *Abies mariesii* and *A. veitchii*, however, two projections are observed only at the middle stages of development. In the mature stage the two projections are changed into a bugle-shape. Thus, the integument of *Pinus* and *Abies* has a peculiar feature in common during the middle stages of development regardless of the shape at the initial and mature stages. That the developing integument has two projections is known also in *Larix europaea* (Baillon, 1864; Strasburger, 1872, 1879), *L. occidentalis* (Owens and Molder, 1979) and *Pseudotsuga menziesii* (Allen, 1963; Allen and Owens, 1972). These facts may suggest that the shape of the integument in the middle stages of development is of some value for the future discussion of the phyletic origin and constitution of the integument.

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Explanation of plates III～IV

Pl. III. *Pinus thunbergii*. Scanning electron micrographs of ovules at various stages of development (A-D: adaxial views, E and F: lateral views). A. The stage when an ovule primordium is being initiated ×95. B and C. A little later stages of A. The integument arises as two distinct swellings on the lateral sides in B and as a horseshoe-shaped swelling in C ×70. D. The middle stage when an ovule has two projections which have been formed by the predominant elongation of the lateral parts of the integument ×50. E and F. The mature stage of ovules. The apical part of the integument shows a two-horned shape ×40, 110.

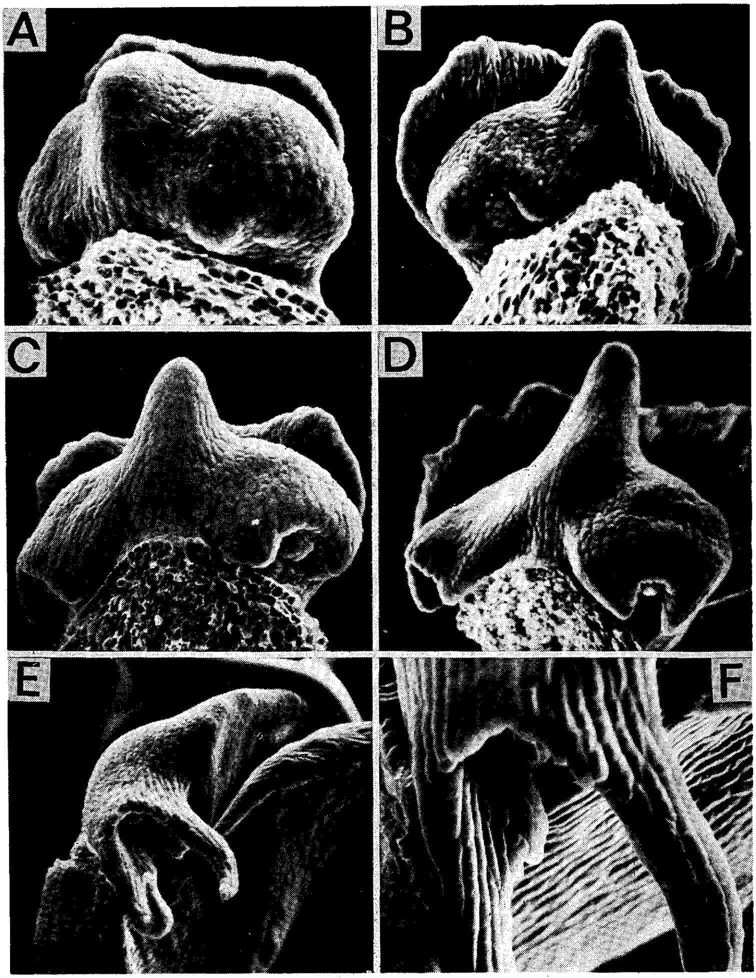
Pl. IV. *Abies mariesii* (A-D) and *A. veitchii* (E-H). Scanning electron micrographs of ovules at various stages of development (A-C and E-G: adaxial views: D: lateral view; H: abaxial view). A. The stage when an ovule primordium is being initiated ×75. B and E. A little later stages of A. The integument arises at several places in B and at two distinct places in E (as pointed out by arrows) ×55, 80. C and F. The stages following B and E respectively ×85, 80. G. The middle stage when an ovule has two projections as in *Pinus thunbergii* ×20. D and H. The mature stage of ovules. The integument is bugle-shaped ×20, 60.

* * * *

本報は裸子植物の珠皮の発生学的研究の第2報である。ここではマツ科の2属3種，クロマツ，オオシラビソ，シラビソを扱った。これらの種では珠皮の発達様式が胚珠上の部位によって異なる。そこで，胚珠上の位置を便宜的に上部，下部及び側部に分けた(Fig. 1).

マツ科では cone の軸上に多数の苞と ovuliferous scale (以下，o.s.) が螺旋状に配列し，各 o.s. の向軸側に2つの胚珠原基が生じる。胚珠原基が o.s. の基部に発達した後，珠皮と珠心が分化してくる。珠皮の initiation は胚珠原基上の“もり上がり”によって認められる。珠皮のもり上がる位置は胚珠により，また種により多少異なる。即ち，クロマツではこのもり上がりが胚珠原基の側部の2か所から現われる例と胚珠原基の下部を除く総ての側から馬蹄形として現われる例がある。また，オオシラビソの一部及びシラビソでは胚珠原基の側部の2か所から現われ，オオシラビソの多くは限定されない幾つかの場所から同時に現われる。これらの珠皮のもり上がりは，クロマツでは主に胚珠原基の表層細胞の並層分裂によって生じ，オオシラビソ，シラビソでは表層細胞の並層分裂と表層下の相当数の細胞分裂によって生ずる。いずれの種でも，珠皮は initiation をした後，発達中期にかけて両側部での活発な生長によって顕著な2つの突起を形成する。この2つの突起は成熟期に及ぶと，クロマツでは2つの角状の突起となる。一方，オオシラビソ，シラビソでは珠皮の上下部の生長も非常に活発になり，2つの突起が次第に不明瞭となり，珠皮はラッパ状を呈する。この様に initiation 時，成熟時の形態に違いがあるにもかかわらず，発達中期に珠皮の2つの突起が共通して現われることから，この形態は珠皮の起源や構成を考察する上で重要な指標と言えるかもしれない。この間の珠皮の生長は主に先端部の表層細胞の並層分裂と表層細胞及び表層下細胞での(珠皮表面に対する)垂層分裂の繰り返しによって起る。したがって，生長期の珠皮の表層下にはしばしば長い細胞列が見られる。また，珠皮の表層下細胞には，特に基部に近い所で並層分裂が起り，珠皮の厚さを増す。成熟した胚珠では，珠皮は完全に珠心を包んで径の大きい珠孔を形成する。受粉後は，クロマツでは珠皮の表皮下細胞が伸長して珠孔を塞ぎ，オオシラビソ，シラビソではラッパ状の珠皮自身が折りたたまれる様にして珠孔を塞ぐ。

前報 (イチョウ) に引き続きクロマツとオオシラビソについても，胚珠の初期生長の間に見られる珠皮及び珠心表層細胞の並層分裂の頻度を調べてみた。その結果，両種ともその頻度は珠皮の側部で最も高く，珠心の先端部，珠皮の上下部の順に減少する。これらの頻度は珠皮の初期生長の様式を良く表わしている。



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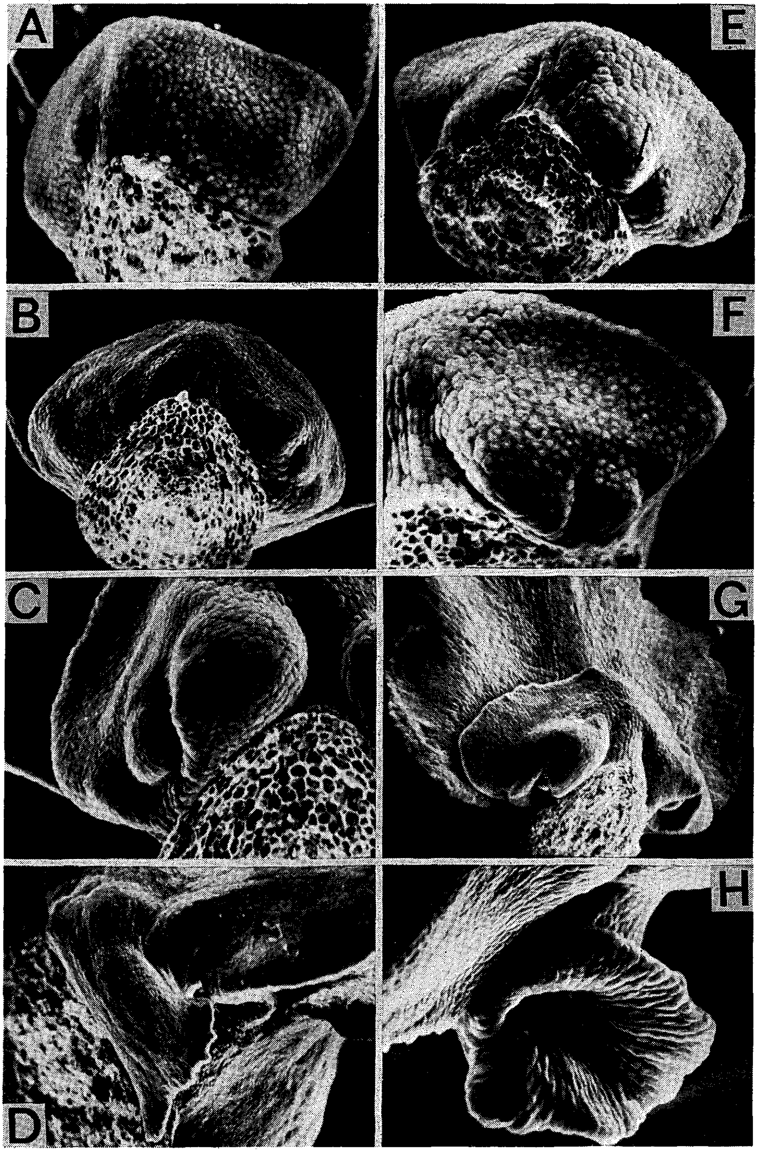

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